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DOES LOWER SALINITY PROVIDE AN ESCAPE FROM HERBIVORY? EFFECT OF DISTANCE FROM A FRESHWATER SEEP ON HERBIVORY OF *THALASSIA TESTIDINUM*

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Abstract: Herbivory is an important determinant of community structure and species distributions in tropical ecosystems. In Discovery Bay, Jamaica, turtle grass (*Thalassia testudinum*) beds are an important source of primary production for the marine ecosystem, and sustain a large population of herbivores. We hypothesized that the freshwater seep in the mangrove area near the Discovery Bay Laboratory may be an escape habitat for plants from herbivores. Using turtle grass leaves as a bioassay, we measured herbivory over a 24-hour period at five different sites along a presumed gradient of decreasing salinity in the mangrove area. Our results suggested that leaf area loss due to herbivory was higher outside the mangrove area than inside, although the trend was not statistically significant. This trend may be due to lower salinity levels in the mangrove than outside, higher damselfish densities in the mangrove than outside, or a limited response to the use of turtle grass, a species not normally found in the mangrove. Future research to clarify whether the mangrove does in fact serve as a refuge from herbivory should consider herbivory on algae that occurs both inside and outside the mangrove.

Key Words: bioassay, escape habitat, mangrove, parrot fish

INTRODUCTION

Herbivory is an important determinant of community structure and the distribution of plant species in tropical marine ecosystems (Hay 1984, Taylor et al. 1986). In these systems, many different habitats may occur over a relatively small area, and there may be distinct differences in levels of herbivory both between habitats (e.g., where reef slopes join sand plains) and within habitats (e.g., in areas of high structural complexity). Locations that provide shelter from herbivory, commonly referred to as escape habitats, may increase the diversity (Hay 1981, Taylor et al. 1986) and the composition (Hay 1984) of benthic plant communities in tropical marine ecosystems.

Turtle grass, *Thalassia testudinum*, is a common plant that grows in shallow waters throughout the Caribbean. In Discovery Bay, Jamaica, turtle grass beds are an important source of primary production for the entire marine ecosystem, and they sustain a large population of herbivores including the sea urchins *Diadema antillarum*, *Lytechinus variegatus*, and *Tripneustes ventricosus*, and the

parrot fish *Scarus croicensis* and *Sparisoma viride* (Ogden et al. 1973, Bizarro et al. 1992). Most turtle grass blades in Discovery Bay display typical round parrot fish bite marks, suggesting that turtle grass is under high herbivory pressure from these fish (Rutar et al. 1997). Therefore, it may be useful to use turtle grass as a bioassay to evaluate the amount of herbivory in different habitats within the Discovery Bay ecosystem.

West of the Discovery Bay Marine Laboratory there is a freshwater seep that empties into a sheltered mangrove area. Water near the freshwater seep is brackish, with salinity ranging between 27 and 33 ppt, but becomes increasingly saline along a gradient toward the sea (34 - 35 ppt; data from the Chemistry Lab, Discovery Bay Marine Laboratory, Jamaica). Many of the herbivores in this system may lack the physiological plasticity in their osmoregulation pathways to accommodate the lower salinity near the freshwater seep, or may simply avoid water of lower salinity. We hypothesized that the mangrove area is an escape habitat for plants from the primary herbivores in Discovery Bay. Using turtle grass as a bioassay, we expected

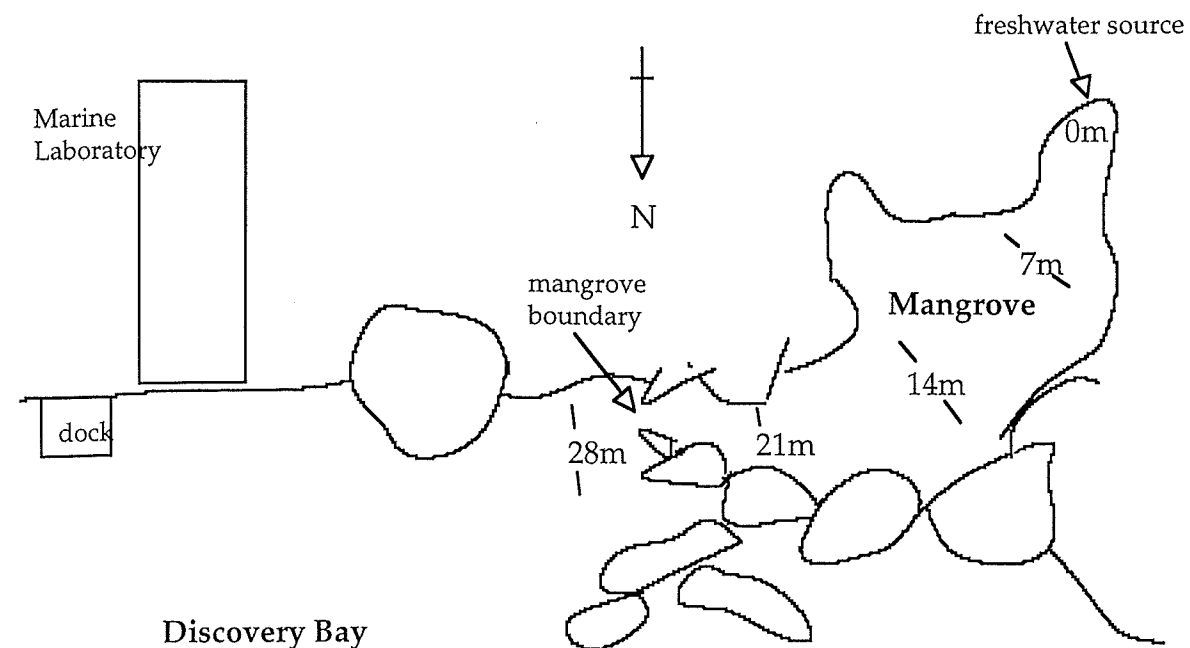


Figure 1. Map of the mangrove area near the Discovery Bay Marine Laboratory, Discovery Bay, Jamaica. Locations of transects are indicated by their respective distance from the freshwater source. The mangrove boundary is indicated at the point where the water becomes very shallow, forming a natural boundary between the pools to the west and Discovery Bay to the east.

to see higher herbivory close to the turtle grass bed compared to areas near the freshwater seep in the mangrove area.

METHODS

We measured herbivory on turtle grass leaves over a 24-hour period in the mangrove area in Discovery Bay, Jamaica. On February 26, 2000, we anchored 5 replicate clusters of uneaten turtle grass (10 leaves per cluster) to the sea floor along each of 5 transects perpendicular to the shore; transects were located in 7 m intervals from the freshwater seep (Fig. 1). We chose turtle grass leaves with similar epiphyte load, and trimmed them along the base until they were uniformly 8 cm long to control for variations within leaves. Grass clusters were anchored on the mangrove floor in $\approx 1.5 - 3$ m of water, > 1 m from the rock edges, and thus away from damselfish territories. 24 hours later we collected and as-

sessed the leaves for herbivory. We determined the percentage of each leaf that had been eaten by comparing the leaves to a gridded leaf template (accuracy $\pm 5\%$). Then we calculated the average amount of herbivory in each replicate. The data were not normal so we compared herbivory among > 2 distances using a Kruskal-Wallis rank sums analysis.

RESULTS

Leaf loss due to herbivory was highest in the transect furthest away from the freshwater seep (which lay outside the mangrove area), although this increase was not statistically significant (Fig. 2; Kruskal-Wallis $\chi^2 = 4.86$, $df = 4$, $p = 0.30$). The amount of variability among replicates increased with distance from the freshwater seep, ranging from 0 - 11% leaf area loss at zero m to 0 - 60% leaf area loss at 28 m. Virtually no herbivory oc-

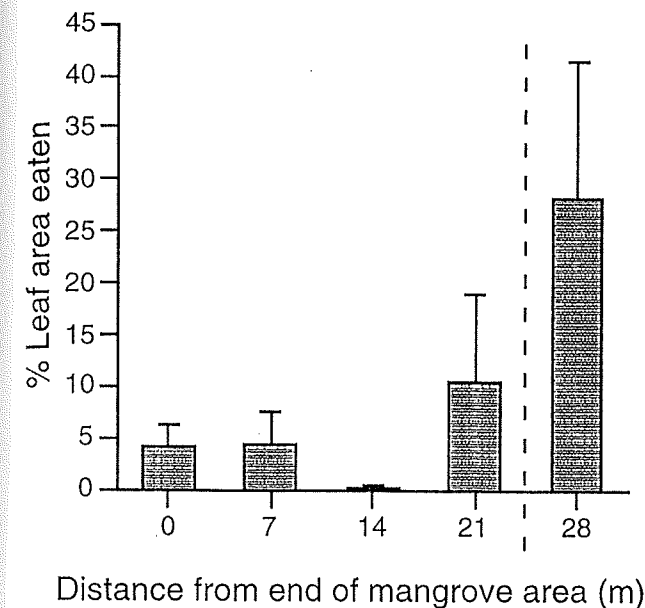


Figure 2. Percent leaf area lost to herbivory over 24 h, in 5 locations of increasing distance from a freshwater source in the mangrove area. Mangrove boundary is marked with a dashed line.

curred along the 14 m transect. Based on the bite patterns on eaten leaves, all leaf loss was presumed to be due to parrot fish herbivory.

DISCUSSION

Herbivory appeared to be higher outside than inside the mangrove area, as predicted (Fig. 2). A possible explanation for this trend is that water with low salinity may prevent herbivorous fish from foraging in the mangrove area. Water salinity increases with distance from the freshwater seep in the mangrove, and stratifies vertically (freshwater is less dense than sea water). Therefore, the narrow channel that marks the boundary of the main mangrove channel should result in lower salinity immediately inside the mangrove area than outside. Freshwater may interfere with osmoregulation in marine fish, or, alternatively, may be avoided. In either case, herbivorous fish abundance, and therefore overall herbivory, would be lower in the mangrove area than outside. Because salinity is lower near the top of the water column, this

trend may be more obvious when tested at higher levels in the water column rather than simply along the bottom.

A second explanation for differences in herbivory is that the greater structural complexity in the mangrove may reduce plant herbivory through its effect on the fish community. It is well-documented that structural complexity increases the availability of suitable damselfish territories, and that damselfish may create a refuge for plants when they defend their territories against herbivorous fish that would feed on the grasses (Foster 1987). Although we did not quantify damselfish density or abundance in this study, many species (*Stegastes fuscus*, and *Stegastes leucostictus*, in particular) appeared to occur at high density in the mangrove area and may inhibit other herbivorous fish from foraging nearby.

Finally, our use of turtle grass, which does not normally grow in the mangrove, limits our ability to extrapolate to herbivory on algae species. More fundamentally, it may have affected the response of herbivorous fish in the mangrove. If herbivorous fish in the mangrove area have a search image for local species, they may not recognize turtle-grass as a food as readily as fish outside the mangrove, where turtle grass occurs more frequently. Thus, a stronger test of our hypothesis would be a similar analysis of herbivory using algal species that occur both inside and outside the mangrove.

Virtually no herbivory occurred along the 14 m transect and we suspect that this, as well as the extreme variability in our data, may be a function of slightly premature leaf collection. Given more time, levels of herbivory may have been more consistent within each transect. Additionally, herbivory at the 14m transect may have been similar to either the 7 m or the 21 m transects because (1) it is unlikely that intermediate salinity would deter herbivory less than lower salinity (i.e., closer

to the freshwater source), and (2), other microhabitat characteristics such as topography or ground cover did not differ markedly from the other transects.

Investigating algal diversity in the mangrove would also be valuable because lower herbivory pressure may result in greater overall algal species diversity (Taylor et al. 1986). Moderate herbivory has been shown to create a type of intermediate disturbance, preventing otherwise dominant species from excluding slower-growing, less-dominant species (Connell 1970, Taylor et al. 1986). In addition, if the mangrove is a refuge habitat, a reciprocal transplant experiment involving algae from both inside and outside the mangrove area could test the hypothesis that the selection for secondary metabolite production may be influenced by herbivory regimes. If algae with high concentrations of secondary metabolites are favored in areas with greater herbivore pressure, we would expect algae from the mangrove to exhibit fewer chemical defenses than algae from habitats with greater herbivory.

In conclusion, our bioassay suggests that the mangrove area may provide a refuge habitat from herbivory, but further study is needed to resolve this question. If the area is a refuge, it raises many possible questions about algal diversity and physiology that may be easily tested in future research. Understanding patterns of herbivory across different habitats is important to understanding the dynamics of macroalgae and plant species throughout this marine ecosystem.

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